

Determining the Optimal Age For Selection by Modelling the Age-Related Trends in Genetic Parameters in *Eucalyptus* Hybrid Populations

By J.-M. BOUVET^{1),*}, P. VIGNERON¹⁾, E. VILLAR^{1),2)} and A. SAYA²⁾

(Received 21th December 2007)

Abstract

Ten factorial mating designs using a combined total of 88 females, 107 males, 684 families and 37,206 individual trees were used to model the age-related trends in genetic parameters and genetic gain between four and 65 months in the *Eucalyptus urophylla* x *grandis* breeding population in Republic of Congo. Selection was either of pure species (as parents for continued breeding) or individual hybrids for commercial plantations based on clonal varieties.

The variance components were significantly different from zero for female, male and female-by-male interaction effects for volume. The age-related trends in additive, dominance and environmental variances, modelled by nonlinear functions, showed three phases corresponding to different stages of competition and growth. Male and female narrow sense heritabilities were high ($h^2_{Am} = 0.70$ and $h^2_{Af} = 0.90$, respectively for highest estimates) compared with individual broad sense heritability ($h^2_{ind} = 0.45$). They were modelled by polynomial functions that did not display specific trends with age.

The age-age correlations, modelled by a response surface, were higher than 0.8 after 36 months. A similar trend with age was observed for additive and total genetic effects.

Genetic gain was calculated by combining the different models. The genetic gain was higher for female than for male. Considerable gains can be achieved by clone selection. The efficiency of selection indicated an optimal age of 54 months for juvenile selection of males and females and a mature age for ortets. The trend in efficiency of selection per time unit showed that juvenile selection for volume is much more efficient than adult selection whatever the age.

Key words: *Eucalyptus*, volume, reciprocal recurrent selection, variance components, heritability, age-age correlation, optimal age of selection.

Introduction

Numerous breeding programmes have been implemented to provide improved germplasm in *Eucalyptus*, which is one of the most important genera used in plantations for pulp wood or charcoal in warm temperate, Mediterranean, and tropical climates. Many of them are based only on assessment of additive effects using open pollinated families to estimate genetic parameters and

genetic gain in the framework of recurrent selection schemes. Examples exist for *Eucalyptus globulus* in Australia (LOPEZ et al., 2001), *E. globulus* in Chile (SANHUEZA et al., 2002), *E. nitens* in Australia (TIBBITS and HODGE, 1998) and in Chile (VELILLA et al., 2007), *E. grandis* in Colombia (OSORIO et al., 2003), and *E. urophylla* in China (WEI and BORRALHO, 1998). For the last twenty years, some eucalyptus breeding programmes have been based on inter-specific hybrids, which at many sites have shown better growth and adaptation than pure species (DE ASSIS, 2000; DALE and DIETERS, 2007; LEE et al., 2007). These programmes have provided numerous clonal varieties, delivered significant gains (VERRYN, 2000), and assessed the relative importance of dominance and additive effects (VOLKER, 1995; LEE et al., 2007; RETIEF and STANGER, 2007). However, results on the relative importance of genetic effects are still few and new experiments are needed to improve our understanding of additive and non-additive genetic effects in hybrid populations.

The *E. urophylla* x *grandis* breeding programme in the Republic of Congo has been promoted for commercial plantations in the southern region of the country. Numerous clones, resulting from a reciprocal recurrent selection strategy (RRS) (VIGNERON, 1991; VIGNERON and BOUVET, 1997; VIGNERON et al., 2000), are currently used to produce pulp wood. However, thanks to the large number of genetic trials, the design of the programme also offered us the opportunity to improve our understanding of the expression of both additive and non-additive age-related effects and their consequences for genetic gain. Better assessment of trends displayed by genetic parameters (variances, heritability, correlations) with age is a key factor in calculating genetic gain and in defining the optimal age for selection.

In this study, we used a large sample of parents, families, and individual trees resulting from 10 factorial mating designs established over 15 years corresponding to the first cycle of the RRS scheme. The general goal was to determine the optimal age for the selection of parents and ortets by modelling trends in genetic selection efficiency. The specific objectives were (i) to assess the age-related changes in the magnitude of additive, non-additive, and environmental variance, (ii) to estimate the trends in age-age correlations, and (iii) to evaluate the genetic gain for parent and ortet selection.

Materials and Methods

Genetic material

Data were obtained from field trials conducted in the Republic of Congo at the UR2PI research centre "Unité

¹⁾ Cirad Biological System Department, Research Unit "Genetic Diversity and Breeding of Forest Tree Species", TA A-39/C Campus International de Baillarguet, 34398 Montpellier Cedex, France. Phone: +33 467-593-728, Fax: +33 467-593-733.

²⁾ UR2PI, Research Unit on the Productivity of Commercial Plantations, BP 1291 Pointe-Noire, Republic of Congo.

^{*}) Corresponding author: JEAN-MARC BOUVET. E-Mail: jean-marc.bouvet@cirad.fr

de Recherche sur la Productivité des Plantations Industrielles du Congo" (04°45'S, 12°00'E, alt 50 m). The climate is tropical humid with a mean annual temperature of 24°C, a mean annual rainfall of 1200 mm (with marked between-year variation, from 500 to 2000 mm) and a dry season from May to October. This study used the same plant material used for the reciprocal recurrent selection scheme for the production of hybrid clones planted in the commercial plantations in the Congo (VIGNERON and BOUVET, 1997). Two species are being used in that scheme: *E. urophylla*, selected for its adaptation to climate and soil conditions, and its resistance to parasites, and *E. grandis*, selected for its rapid growth during the juvenile stage and its straight stem. *E. grandis*, used as the pollen parent, was sourced from the northern part of its natural range, in Queensland, Australia. The males of *E. grandis* were selected at adult stage for their growth, adaptation and stem straightness. The females of *E. urophylla* were sourced from a range of provenance trials established in the Congo from 1971 to 1986. The first *E. urophylla* parents were selected for their abundance of flowers (in many cases they were border trees that benefited from more light) or for their early growth one or two years after planting. Progressively, *E. urophylla* females were selected for their growth, stem form or adaptation as adults. Selected trees of both species were grafted into seed orchards. Crosses were made by controlled pollination (BOUVET, 1982) using a factorial mating design with *E. urophylla* as females and *E. grandis* as males. Owing to technical problems, the mating design was not complete and not correctly balanced: for most of the mating designs, the ratio of full cells to total cells was less than 50% (see Table 1). The plants were grown in the UR2PI nursery in Pointe-Noire. The seeds were sown on a sandy substrate and the two-leaf seedlings were transferred to small containers. After three months, the seedlings had reached an average height of 40 cm and were ready for planting.

The hybrid families were planted at 4 m x 4 m spacing (625 trees/ha). This is low stocking for a short rotation pulpwood crop, but this is the density used by commercial plantations and was determined by previous silvicultural research. Within each field trial, the experiment was an incomplete block design with 16-tree square plots in four replicates. To minimize edge effects, two border rows were planted around the trial plots. From 1989 to 2001, ten factorial mating designs were constructed and planted in the same zone in a single site. A total of 88 different females, 107 males, 684 full-sib families and 37,206 individuals (Table 1) were established in this first cycle of RRS.

Measurements

Circumference at breast height (1.3 m) and total height were used to calculate volume using a conic function. Trial measurement ceased after ortet selection (varying from 36 to 50 months old), and shoots were collected from the stumps of the "plus" trees to provide the first ramets of clones. The number of measurements varied from one trial to another (Table 1).

Estimation of variance components

Data analyses were conducted after removing outlier trees such as dwarfs (very small trees with abnormal architecture). As the mating designs were connected by only one or two parents, and because the measurements were made at different ages in the trials (Table 1), analyses of variance were performed independently for each trial. The average trend in variance was modelled using a nonlinear equation. For the analysis of each mating design, we used the following mixed model (BOUVET et al., 2008):

$$y_{ijkl} = \mu + m_i + f_j + m^*f_{ij} + b_k + m^*f^*b_{ijk} + r_{ijkl} \quad (\text{model 1})$$

where y_{ijkl} is the l^{th} tree in the k^{th} block resulting from the cross of the i^{th} male in the j^{th} female,

μ is the overall mean,

m_i is the random effect of male i with variance σ_m^2 and an expectation of 0,

f_j is the random effect of the j^{th} female, with variance σ_f^2 and an expectation of 0,

m^*f_{ij} is a random effect of the male i by female j interaction with variance $\sigma_{m^*f}^2$ and an expectation of 0,

b_k is the effect of the k^{th} block considered as fixed,

$(m^*f^*b)_{ijk}$ is the male-by-female-by-block interaction effect with variance σ_{plot}^2 and an expectation of 0 which estimates the environmental effect common to all the individuals planted in the same plot (GALLAIS, 1989),

r_{ijkl} is the residual random effect with variance σ_r^2 and an expectation of 0 which estimates the confounded genetic and environmental effect common to all the individuals planted in the same plot.

The variance components were estimated using the SAS VARCOMP procedure and the REML (restricted maximum likelihood) method of the SAS/STAT® software (SAS INSTITUTE, 1990). The relationship between variance components and the quantitative genetic model was used to estimate the additive and dominance variance (GALLAIS, 1989).

$\sigma_{Am}^2 = 4*\sigma_m^2$ is the additive variance due to the male effect,

$\sigma_{Af}^2 = 4*\sigma_f^2$ is the additive variance due to the female effect,

$\sigma_A^2 = 1/2 (\sigma_{Am}^2 + \sigma_{Af}^2)$ or $\sigma_A^2 = 2*(\sigma_m^2 + \sigma_f^2)$ is the additive variance combining the male and female effects,

$\sigma_D^2 = 4*\sigma_{m^*f}^2$ is the dominance variance,

$\sigma_{env}^2 = \sigma_{plot}^2 + [\sigma_r^2 - (1/2 \sigma_A^2 + 3/4 \sigma_A^2)]$ is the environmental variance estimated by combining within-plot and between-plot environmental variance,

$\sigma_G^2 = \sigma_A^2 + \sigma_D^2$ or $\sigma_G^2 = 2*(\sigma_m^2 + \sigma_f^2) + 4*\sigma_{m^*f}^2$ is the total genetic variance,

$\sigma_{phen}^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{env}^2$ is the total phenotypic individual variance.

Various variance ratios were analysed: (σ_D^2/σ_A^2) is the ratio of dominance to additive variance and (σ_m^2/σ_f^2) is the ratio of male additive to female additive variance.

Calculation of correlations

To calculate the age-age correlations, we estimated the genetic and residual variance and co-variance compo-

nents between two ages with the SAS GLM procedure (MANOVA option) and the Type III sums of squares (SAS INSTITUTE Inc. 1990). The variance and covariance components were estimated by equating the expected mean square (calculated by the RANDOM option) to the mean square given by type III of analysis of variance (BECKER, 1984).

$\sigma_{(age1, age2)}$ being the covariance between volume at age1 and volume at age2, $\sigma_{(age1)}^2$ and $\sigma_{(age2)}^2$ being the variance at age1 and age 2, three correlations can be estimated:

the male additive correlation

$$\rho_{Am(age1/age2)} = \frac{\sigma_{Am(age1,age2)}}{\sigma_{Am(age1)} * \sigma_{Am(age2)}},$$

the female additive correlation

$$\rho_{Af(age1/age2)} = \frac{\sigma_{Af(age1,age2)}}{\sigma_{Af(age1)} * \sigma_{Af(age2)}}$$

the total genetic correlation

$$\rho_{G(age1/age2)} = \frac{\sigma_{G(age1,age2)}}{\sigma_{G(age1)} * \sigma_{G(age2)}}$$

Calculation of heritabilities

h_{Af}^2 is the narrow sense heritability based on the mean female progeny:

$$h_{Af}^2 = \frac{1 / 4 \sigma_{Af}^2}{\sigma_f^2 + \frac{\sigma_{m*f}^2}{m'} + \frac{\sigma_{plot}^2}{b' m'} + \frac{\sigma_r^2}{b' m' n'}} \quad (\text{eq. 1})$$

Where m' is the harmonic mean of males crossed with one female, b' is the harmonic mean number of repetitions and n' is the harmonic mean number of trees per plot.

h_{Am}^2 is the narrow sense heritability based on the mean male progeny:

$$h_{Am}^2 = \frac{1 / 4 \sigma_{Am}^2}{\sigma_m^2 + \frac{\sigma_{m*f}^2}{f'} + \frac{\sigma_{plot}^2}{b' f'} + \frac{\sigma_r^2}{b' f' n'}} \quad (\text{eq. 2})$$

Where f' is the harmonic mean of females crossed with one male, b' is the harmonic mean number of repetitions and n' is the harmonic mean number of trees per plot.

H_{ind}^2 is the broad sense heritability based on individuals:

$$H_{ind}^2 = \frac{2(\sigma_m^2 + \sigma_f^2) + 4\sigma_{m*f}^2}{2(\sigma_m^2 + \sigma_f^2) + 4\sigma_{m*f}^2 + \sigma_{env}^2} \quad (\text{eq.3})$$

Modelling trends in genetic parameters with age

We used nonlinear and polynomial models to assess the general trend in variance components, variance ratio and correlations. Numerous classic models were tested using the Xlstat-Pro® version 7.5 (Addinsoft, France, Paris: www.xlstat.com). Based on the determination coefficient, we selected the following non linear model for modelling the variance components with age:

$$\sigma_m^2 \text{ or } \sigma_f^2 \text{ or } \sigma_{m*f}^2 \text{ or } \sigma_{env}^2 \text{ or } \sigma_{phen}^2 = \frac{a}{(1 - e^{-b} - c * age)} \quad (\text{model 2})$$

For the trends in heritability, we used a polynomial equation of degree 2.

$$H_{ind}^2 \text{ or } h_{Af}^2 \text{ or } h_{Am}^2 = a + b * age + c * age^2 \quad (\text{model 3})$$

For the age-age correlation, the model was based on the response surface method (MEYERS and MONTGOMERY, 2002). The coefficients were estimated using the SAS procedure PROC RSREG (SAS INSTITUTE, 1990) to estimate a surface response. The surface we used to model the age-age correlation was as follows:

$$\rho_{age1/age2} = a + b * age_1 + c * age_2 + d * age_1^2 + e * age_2^2 + f * age_2 * age_1 \quad (\text{model 4})$$

For the three models, an adjustment was made by weighting each estimate of the variance ratio with the number of crosses made in each mating design (Table 1). This procedure takes into account the accuracy of each estimate. The method of weighting used, the estimations of coefficients (a, b, c, d, e and f) and the calculation of associated probability for testing the significance of the model were done with the NLIN and REG procedures of the SAS software (SAS INSTITUTE, 1990).

Calculation of genetic gain and selection efficiency

Classic formulas were used to calculate the gain at the adult stage (age 2) (72 months in the case of these plantations and the corresponding improvement programme) and the correlated genetic gain by a selection at younger stages (OSORIO et al., 2003). The values of parameters over time were given by the different models [1 to 4]. In the reciprocal recurrent selection strategy, two types of selection need to be considered: the selection of parents for the intra-species recombination phase and the selection of ortets for the development of clonal varieties.

Gain, as a percent of population mean, when selecting at age 2 (age 2 = rotation age, i.e., 72 months):

$$\Delta G_{age2} = \frac{i * H_{age2}^2 * \sigma_{phen/age2}}{\text{trait mean}_{age2}} * 100, \quad (\text{eq. 4})$$

Gain at age 2 as a percent of population mean, when selecting at age 1 (age 1 = considered as the juvenile stage):

$$\Delta G_{age1/age2} = \frac{i * H_{age1} * \rho_{(age1/age2)} * H_{age2} * \sigma_{phen/age2}}{\text{trait mean}_{age2}} * 100, \quad (\text{eq.5})$$

Where “i” is the intensity of selection expressed as standard deviation (GALLAIS, 1989), $\rho_{(age1-age2)}$ is the genetic correlation between age1 and age2 (rotation age), $H_{age1 (age2)}$ is the square root of the heritability at age1 (age2), $\sigma_{phen/age2}$ is the square root of the phenotypic variance at age2.

To analyse the efficiency of juvenile selection we applied two approaches commonly used in forest tree breeding (JOHNSON et al., 1997; ADAMS et al., 2001): the efficiency of juvenile selection “E” when selecting at age1 to predict gain at age2 defined in previous studies (OSORIO et al., 2003) by:

$$E = \frac{\Delta G_{age1/age2}}{\Delta G_{age2}} \quad (\text{eq.6})$$

and the gain efficiency per time unit “ E_t ” when selecting at age1 to predict gain at age2 (LEE et al., 2001) defined by:

$$E_t = \frac{\Delta G_{age1/age2}}{\Delta G_{age2}} * \frac{age2}{age1}, \quad (\text{eq.7})$$

Results

Growth of the Eucalyptus hybrid

The trials were differently affected by mortality, but mortality was generally moderate after the first year and was lower than 16% at 72 months old (Table 1). At

72 months, with a density of 625 trees/ha, the mean stem volume was 150 dm³/tree. The increase in volume was moderate, (see Table 1) due to the poor sandy soils of the region. The range in volume was significant between some experiments and the two extremes at 67 months were represented by trial R90-11 with a mean individual volume VI = 135.44 dm³ and trial R99-2 with an individual volume VI = 196.89 dm³. However, we were unable to attribute this difference to the soil, climatic factors, or to the genetic performances of plant material used in the different mating designs.

Trends in variances

The analyses showed that the variances were significantly different from zero for the three genetic effects (results not shown), indicating marked variability with-

Table 1. – Main characteristics of the mating designs, age of measurement, trend in mean volume and mortality with age for each plan.

Year of planting	plan	Full cells/total cells (%)	Number of full- sib families	Number of <i>E. urophylla</i> females	Number of <i>E.</i> <i>grandis</i> males	Number of trees in the trial	Age at measurement (months)	volume (dm3)	mortality (%)
1989	R89-20	37	50	15	9	2144	18	13.36	10.2
							29	35.25	15.3
							36	56.89	15.5
							42	71.00	15.6
							48	87.51	15.7
1990	R90-11	45	94	16	13	4828	15	5.33	9.5
							27	25.81	10.2
							38	47.82	10.5
							67	135.44	12.5
1991	R91-7	60	38	9	7	2048	19	14.55	9.6
							24	27.67	9.7
							39	64.60	9.8
							50	98.87	10.2
1992	R92-4	46	121	20	13	6464	35	62.92	13.6
							48	120.11	14.4
1995	R95-7	15	126	29	29	6928	19	12.23	9.8
							35	52.99	10.8
1996	R96-3	19	60	15	15	3120	24	31.48	6.9
							38	65.74	9.1
1997	R97-5	27	72	7	18	4800	14	11.13	6.0
							34	72.87	7.1
							39	94.73	7.6
							48	123.44	8.0
1999	R99-2	33	52	12	13	2816	12	7.15	4.9
							24	38.93	6.4
							49	134.99	11.2
							65	196.89	15.7
2000	R00-1	65	26	5	8	1750	13	9.08	4.6
							40	102.30	10.0
							61	171.74	12.0
2001	R01-1	47	45	6	16	2308	24	42.63	2.9
							40	99.18	6.7
							48	117.92	7.8
total			684	88 ⁽¹⁾	107 ⁽¹⁾	37206			

⁽¹⁾ This is the number of different females and males used in the mating design. This number is smaller than the column total because some males and females are repeated in several mating designs.

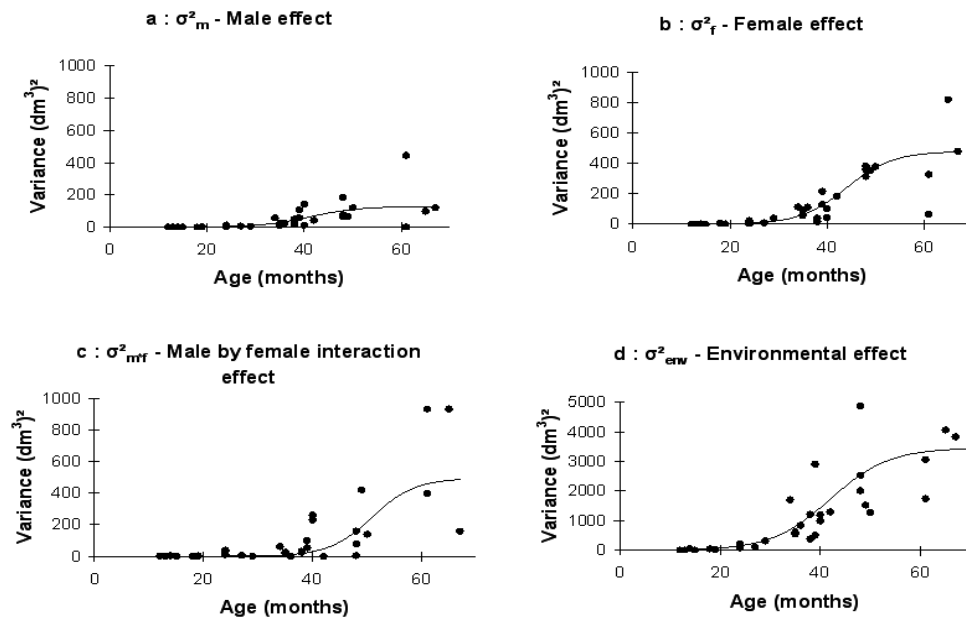


Figure 1. – Trend in variance with age for *E. urophylla* x *grandis* for volume growth. The curve was modelled using a nonlinear function (model 2) weighted by the number of crosses per mating design.

- a: σ_m^2 – male effect,
 b: σ_f^2 – female effect,
 c: σ_{mf}^2 – male by female interaction effect.
 d: σ_{env}^2 – environmental variance estimated by combining within-plot and between-plot environmental variance.

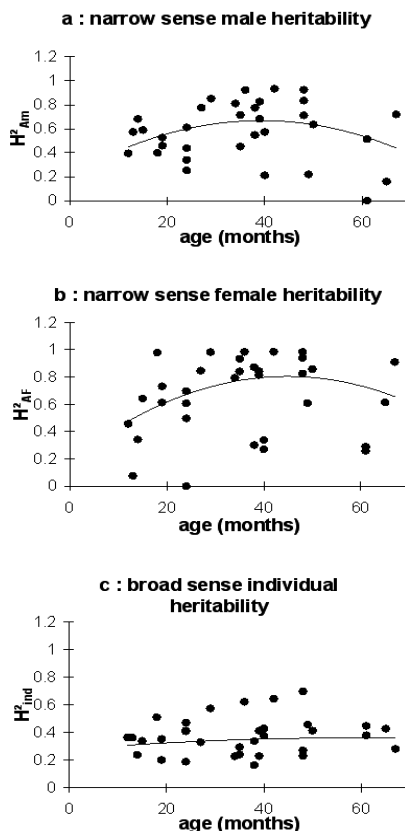


Figure 2. – Trend in heritability with age for volume. The curve was modelled using a polynomial function (model 3) weighted by the number of crosses per mating design.

- a: narrow sense male heritability
 b: narrow sense female heritability
 c: broad sense heritability

in the hybrid population. Adjustment with the nonlinear model resulted in relatively high coefficients of determination (0.460 to 0.762) with probabilities lower than 0.001 (Table 2), indicating that the nonlinear model [2] fitted the general trend with acceptable accuracy. However, Figures 1a to 1d illustrate substantial dispersion of values around the curve, highlighting the effect of the factorial design (sample, year, location) on the estimate of variance. The variance trends suggested three periods related to three stages of growth (Fig. 1). During the first period, from planting to 24 months (juvenile stage), variance increased slowly and remained weak. The second period, from 24 to 48 months (mid-rotation stage), was associated with a rapid increase in variance, and the third period from 48 to 72 months (adult stage) corresponded to a plateau or a slow increase in variance.

The male variance was generally smaller than female variance. The σ_m^2/σ_f^2 ratio decreased with age from one at 12 months to 0.5 at 67 months (results not shown). The dominance to additive variance ratio (σ_D^2/σ_A^2) displayed values higher than one with some estimates close to 3 at the young and adult stages (results not shown).

Trends in heritability

The three heritabilities did not exhibit marked trends with age (Fig. 2 a, b and c). The coefficient of determination was small (0.072; 0.206; 0.116) for h_{Am}^2 , h_{Af}^2 and H_{ind}^2 , respectively and the model was only significant for h_{Af}^2 ($P = 0.031$) (Table 2), stressing the strong dispersion of estimates around the model and highlighting the impact of sample size on the accuracy of estimates. Modelled female heritability was higher than male heritabil-

Table 2. – Coefficient of determination R^2 , coefficients of model (a, b, c, d, e and f), and their standard deviation (between brackets) of the different models used to fit the trends in the various genetic parameters with age Prob: Probability associated with the Fisher test for the significance of the model.

Genetic parameter	model	Model parameter variance components				
			Female effect σ^2_f	Male effect σ^2_m	Male by female interaction effect σ^2_{m+f}	Environmental effect σ^2_{env}
Variance component	Nonlinear (2)	Prob	<0.001	<0.001	<0.001	<0.001
		R ²	0.762	0.460	0.532	0.595
		a	-9.189 (2.318)	-8.241 (4.478)	-12.858 (9.942)	-6.519 (2.327)
		b	0.209 (0.057)	0.200 (0.119)	0.253 (0.211)	0.147 (0.061)
		c	479.412 (56.123)	128.578 (29.042)	494.458 (101.914)	3365.309 (676.962)
Model parameter heritability						
Heritability	Polynomial (3)		Narrow sense female heritability h^2_{Af}	Narrow sense male heritability h^2_{Am}	Broad sense individual heritability H^2_{ind}	
		Prob	0.031	0.326	0.159	
		R ²	0.206	0.072	0.116	
		a	0.201 (0.199)	0.195 (0.192)	0.173 (0.088)	
		b	0.026 (0.011)	0.018 (0.011)	0.002 (0.005)	
c	-2.824E-4 (1.423E-4)	2.26E-4 (1.38E-4)	3.872E-7 (0.67E-5)			
Model parameter age-age correlation						
Correlation	response Surface (4)		Female additive effect ρ_{Af}	Male additive effect ρ_{Am}	Total genetic effect ρ_G	
		Prob	<0.001	<0.001	<0.001	
		R ²	0.316	0.522	0.599	
		a	0.932698 (0.072)	0.930651 (0.034)	0.931481 (0.042)	
		b	5.73E-4 (34.86E-4)	10.99E-4 (17.38E-4)	4.78 E-4 (20.36E-4)	
		c	5.73E-4 (34.86E-4)	10.99E-4 (17.38E-4)	4.78 E-4 (20.36E-4)	
		d	-1.30E-4 (0.45E-4)	-1.12E-4 (0.23E-4)	-1.37E-4 (0.26E-4)	
		e	2.70E-4 (0.37E-4)	2.13E-4 (0.20E-4)	2.85E-4 (0.21E-4)	
f	-1.30 E-4 (0.45E-4)	-1.12E-4 (0.23E-4)	-1.37E-4 (0.26E-4)			

ity $h_{Af}^2 = 0.90$ compared to $h_{Am}^2 = 0.70$ for the highest point of the curve, possibly explained by higher variability of the female population (Fig. 1a, b). Heritability calculated on the basis of individual phenotype was smaller ($H_{ind}^2 = 0.45$ for the highest point of the curve), because the environmental effects are preponderant at an individual level (Fig. 2c).

Age-age correlation

Our modelling of age-age correlation with a response surface gave acceptable results, with the coefficient of determination around 0.3 for the female effect, 0.5 for the male effect, and 0.6 for the total genetic effect. All three models were significant (Table 2). As expected, the correlation of the male and female additive, and total genetic effects showed a marked increase (Fig. 3a, b and c). After 36 months, the values were higher than 0.8. These high age-age genetic correlations confirm previous findings in eucalyptus populations. (BOUVET, 1995; OSORIO et al., 2003)

Genetic gain and optimal age for selection

Although all the models for heritability were not significant (Table 2), we used the equation [5] to calculate genetic gain. For males (Fig. 4a) and females (Fig. 5a), the genetic gain increased with age and reached an optimum around 54 months. The genetic gain for females was higher than that for males (14% and 6% respectively for 30% selection intensity at 54 months). This may be explained by the higher genetic variability and heri-

tability of the female breeding population (Fig. 1 and 2). The results are presented with two moderate intensities of selection (30 and 50% of trees selected are used for the second cycle of RRS) so as to prevent genetic erosion in further breeding cycles (GALLAIS, 1989). For the males and females, the efficiency of selection “ E ” was close to one at 30 and 42 months respectively (Fig. 4b and 5b), suggesting that this age is appropriate for screening of males and females. Values higher than one and trend of the curve after 42 months showed that the optimal age of selection is 54 months and not 72 months, i.e. the rotation age. The decrease in the gain efficiency between 54 and 72 months may be explained by a decrease in heritability with age between 54 and 72 months (Fig. 2a and 2b).

The efficiency of selection per time unit “ E_t ” decreased rapidly with age, especially before 18 months, but was higher than one from 6 up to 72 months for male and female selection (Fig. 4c and 5c). For example, at 24 months, the genetic gain per time unit was 3 (2.5) times higher than the gain at adult stage for male and female selection respectively.

For the selection of individual trees (ortets), the results suggest that considerable genetic gain can be achieved (40 and 60% of the population mean at 72 months for an intensity of selection of 5 and 1%, respectively) (Fig. 6a). This result is to be expected because of the marked variability within the *Eucalyptus* hybrid population which had not undergone previous breeding

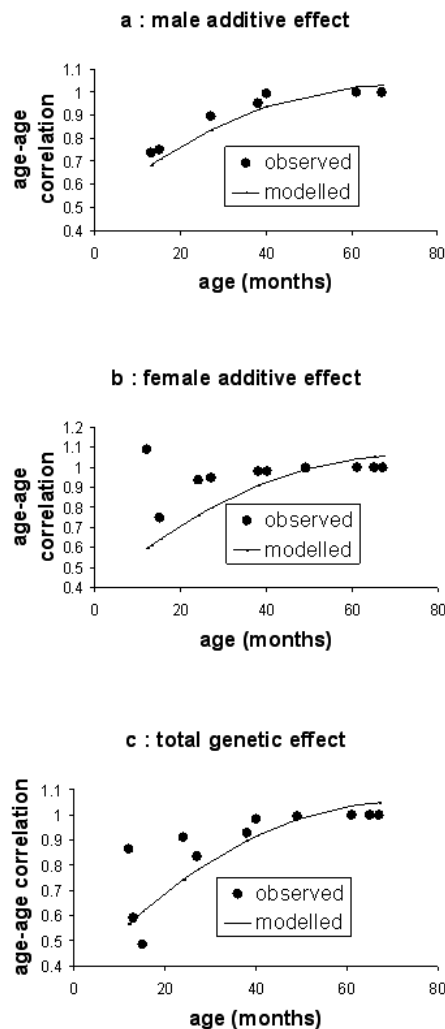


Figure 3. – Trend in age-age correlation with age for volume. The curve was modelled using a response surface (model 4) function weighted by the number of crosses per mating design.

a: male additive age-age correlation
b: female additive age-age correlation
c: total genetic age-age correlation

cycles, the high selection intensity (1 and 5% of trees selected) and the exploitation of both additive and dominance effects. The efficiency of selection “ E ” was lower than one from 6 up to 72 months suggesting a better efficiency of selection at adult stage (Fig. 6b). However, the efficiency of selection per time unit “ E_t ” was higher than one from 6 up to 72 months (Fig. 6c). At 24 months, the genetic gain per time unit was 1.5 times higher than the gain at adult stage.

Discussion

Although calculation of genetic gain and determination of optimal age for selection in programmes using both additive and non-additive effects have been studied in various *Eucalyptus* breeding programmes (VOLKER, 1995; REZENDE and DE RESENDE, 2000; LEE et al., 2007; RETIEF and STANGER, 2007) new results are needed to improve our understanding of the influence of additive and non additive effects in growth traits and their con-

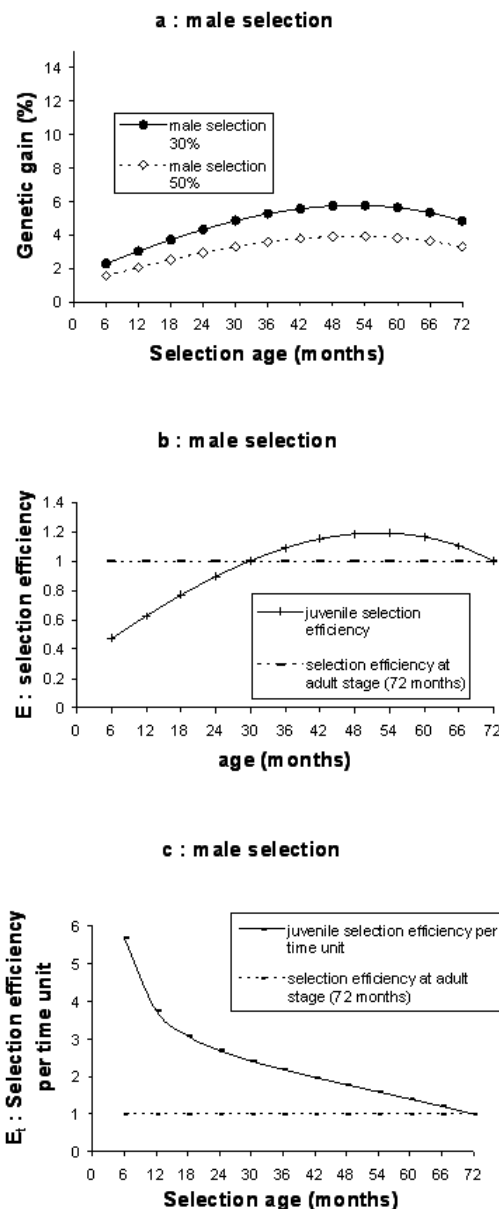


Figure 4. – Trends in genetic gains with age (a), in the efficiency of selection (b) and in the efficiency of selection per time unit (c) for male selection.

sequences for the optimal age for selection. Our study provides new empirical results in the context of tree breeding, especially for *Eucalyptus*, one of the most widely planted tree genera in tropical and warm temperate zones.

Trends in variance components

The variance trends suggested the presence of three periods. During the first period, from planting to 24 months, variance increased slowly and remained weak. This may be explained by growth being directed towards exploitation of the environment by the seedling's root system. During this period, the root system develops rapidly in *Eucalyptus* in the conditions prevailing in the Congo (BOUILLET et al., 2002). During the second period, from 24 to 48 months, there was a rapid increase in

variance, corresponding to a period of increasing growth and competition. During the third period, the rate of increase in variance decreased, corresponding to a slower growth once competition is established. This analysis clearly showed that variance expression is related to growth and competition, as suggested by Franklin's model (FRANKLIN, 1979) in other species. Variance after 65 months of age could not be assessed in these experiments because of the rotation age of *Eucalyptus* trials. However, a longer study (150 months) with clones using wide spacings, (BOUVET, 1991), indicated that variance increases slowly with age in *Eucalyptus* stands in the Congo, but that the coefficient of variation remains relatively stable over time (very small increase after 50 months of age). We can suppose the same trend after 65

months in our present field trials as we planted with the same wide spacing (625 trees/ha), corresponding to the spacing used in commercial plantations to prevent strong competition

The analysis indicates a σ_D^2/σ_A^2 ratio higher than one from planting to 60 months of age. These results are consistent with previous studies with height and circumference on the same sample (BOUVET et al., 2009). The authors suggest that this slight preponderance of the dominance effect can be explained by the effect of the phenotypic selection of female and male parents (BOUVET and VIGNERON, 1996) and the expression of the overdominance in the case of hybrids (BIRCHLER et al., 1990), especially when they are planted in marginal zones where hybrid vigour plays an important role in

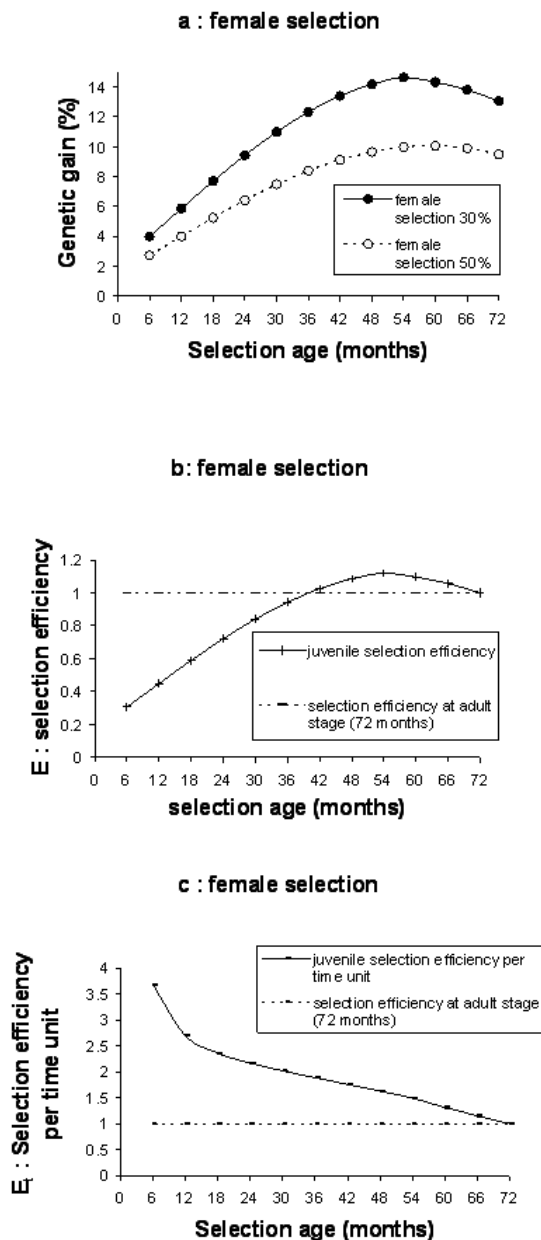


Figure 5. – Trends in genetic gains with age (a), in the efficiency of selection (b) and in the efficiency of selection per time unit (c) for female selection.

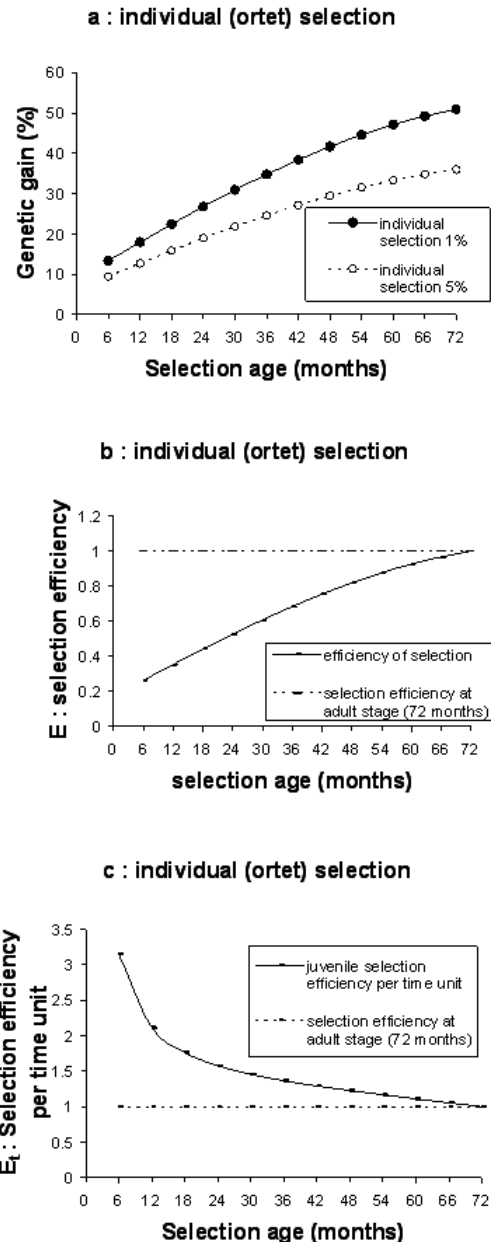


Figure 6. – Trends in genetic gains with age (a), in the efficiency of selection (b) and in the efficiency of selection per time unit (c) for individual (ortet) selection.

adaptation and performance (POTTS and DUNGEY, 2004; DALE and DIETERS, 2007).

Heritability of volume

Our results showed that narrow and broad sense heritabilities varied moderately during the young and mature stages (Fig. 2 and Table 2). This result is consistent with studies on some tropical and temperate species (BORRALHO et al., 1992a; MARQUES et al., 1996; PATINOT-VALERA and KAGEYAMA, 1995; WEI and BORRALHO, 1998). The absence of trends may be due to the short period taken into account in stand development. Although our trials represented good testing conditions (effective weed control, fertilisation), the individual broad sense heritabilities for volume, H^2_{ind} , were significant but relatively small (0.35 on average) compared to other studies (VOLKER et al., 1990; BORRALHO et al., 1992b; TIBBITS and HODGE, 1998; SANHUEZA et al., 2002). This may be explained by the strong micro-environmental effect due to mortality during tests (Table 1), leading to a variable competition effect among trees, especially for growth traits (GALLAIS, 1989; FALCONER and MACKAY, 1996). Conversely, our estimates of narrow sense heritability for parent selection, h^2_{Am} and h^2_{Af} , are quite high compared with the same studies. The large number of progenies per parent combined with the good testing conditions and the four replications used in most of the trials may account for this result.

Consequences for genetic gain and optimal age of selection

In the context of the reciprocal selection scheme, the objective is to select parents for recombination for the next breeding cycle and to select individuals (ortets) for the production of clones. Modelling of age-related trends in genetic parameters has been used to calculate genetic gain with different selection intensities, and to determine the optimal age for selection.

The optimal age for selection has been reported in different breeding programmes for short rotation plantations: 12 months for height and circumference in *E. urophylla* (WEI and BORRALHO, 1998), 30 months for circumference (MARQUES et al., 1996) and 36 months for *E. grandis* (OSORIO et al., 2003). In our study, the efficiency “E” indicated an optimal age of 54 months for juvenile selection for males, females and mature age for ortets. However, the efficiency per time unit “ E_t ” showed that juvenile selection is more efficient than adult selection whatever the age for females, males and ortets especially before two years. A similar result in “ E_t ” trend was observed in previous study in Sitka Spruce (LEE et al., 2001). The efficiency of juvenile selection is explained by the high heritability at younger stages and the strong age-age genetic correlation. In preliminary analyses, BOUVET (1995) suggested that 36 months old could be an appropriate age for juvenile selection. Our more global results offer new elements to adjust the optimal age of selection. This age should be decided by taking into account the trend in efficiency of selection per time unit with age for volume, but also the efficiency of selection of others traits important for eucalyptus breeding (wood properties, diseases resistance).

Equations 4 and 5 show that increasing heritability and age-age correlations can increase the genetic gain. Numerous studies have analysed ways to increase these parameters, for example by changing competition (by increasing plantation density) in *Eucalyptus* progeny tests (BOUVET et al. 2003; 2005). These authors showed that increased competition can improve genetic gain, but the relationship depends on the field design (single tree plot versus square plot) and on the genotype (families versus individuals). For the selection of individual trees (ortets) the use of an experimental design with a density, fertilising regime and silviculture similar to the commercial plantation is recommended.

In this study, we also considered another critical parameter, i.e. the intensity of selection. The intensity of selection for females and males was not very strong (two scenarios with 30 and 50% of trees selected for the second RRS cycle). This moderate intensity prevents genetic erosion in further breeding cycles, which is critical for long-term breeding (GALLAIS, 1989). A moderate intensity of selection on growth traits is also recommended in order to maintain breeding potential for other traits such as wood properties. Due to the absence of a strong correlation between basic density and growth traits, (BOUVET, 1995; BOUVET and BAILLERES, 1995; TIBBITS and HODGE, 1998; SANHUEZA et al., 2002) a broad genetic base is required to increase the probability of selecting individuals with combinations of favourable traits. For individual trees, we chose a stronger selection intensity (1 and 5% of trees selected) leading to considerable genetic gain, given that the objective is to create clonal varieties. As with the parents, the selection intensity should be lower in a multi-trait approach especially with uncorrelated traits (such as basic density) in order to detect ideotypes (BARADAT et al., 1994).

Conclusion

The breeding strategy implemented in the Congo was chosen to optimise the selection process based on both additive and non-additive effects. The importance of both additive and dominance effects in the expression of volume, based on the consistent sampling of parent trees, families and individuals, confirmed that the reciprocal recurrent selection scheme was a relevant choice for the improvement strategy. The objective of our study was both to predict genetic gain for volume according to different selection scenarios, and to propose a frame to determine (and adjust) the optimal age for selection using the information obtained at the end of the first cycle of the breeding strategy. The study shows that juvenile selection per time unit of parents and clones for volume can be more efficient than selection at rotation age in the Congolese eucalyptus breeding programme.

Acknowledgements

We are grateful to the three founders of the UR2PI (*Unité de Recherche sur la Productivité des Plantations Industrielles*) in the Republic of Congo for having supported this research over a period of several years: the Ministry of Research of the Republic of the Congo, the plantation company (*Eucalyptus Fibre* of the Congo) EFC and

the CIRAD. We are grateful to the UR2PI staff, especially the monitoring team, for providing information and data on the experimental designs. We are grateful to the three anonymous reviewers for their suggestions and comments, which significantly improved the manuscript.

References

- ADAMS, W. T., S. N. AITKEN, D. G. JOYCE, G. T. HOWE and J. VARGAS-HERNANDEZ (2001): Evaluating Efficacy of Early Testing for Stem Growth in Coastal Douglas-fir *Silvae Genetica* **50**: 167–175.
- BARADAT, P., T. LABBE and J.-M. BOUVET (1994): Conception d'index pour la sélection réciproque récurrente: aspects génétiques, statistiques et informatiques. Pages 101–150. *In*: Traitements statistiques des essais de sélection. Stratégies d'amélioration des plantes pérennes. Actes du séminaire de biométrie et génétique quantitative. CIRAD, Montpellier, France.
- BECKER, W. A. (1984): Manual of Quantitative Genetics, 4th edn, p 188 Academic Enterprises, Pullman, Washington.
- BIRCHLER, J. A., H. YAO and S. CHUDALAYANDI (2006): Unraveling the genetic basis of hybrid vigor. *P Natl Acad Sci USA* **103**: 12957–12958.
- BORRALHO, N. M. G., P. J. KANOWSKI and P. P. COTTERILL (1992a): Genetic control of growth of *Eucalyptus globulus* in Portugal. I Genetic and phenotypic parameters, *Silvae Genetica* **41**: 39–45.
- BORRALHO, N. M. G., P. J. KANOWSKI and P. P. COTTERILL (1992b): Genetic parameters and gain expected from selection for dry weight in *Eucalyptus globulus* ssp. *Globulus* in Portugal. *Forest science* **38**: 80–94.
- BOUILLET, J. P., R. SAFOU-MATONDO, J.-P. LACLAU and J. RANGER (2002): Changes with age in the spatial localisation of roots of an *Eucalyptus* clone in the Congo. Impact on water uptake ability. *Forest Ecology and Management*. **171**: 43–57.
- BOUVET, J.-M. (1982): Pollinisation contrôlée des Eucalyptus et production d'hybrides en République Populaire du Congo : Mémoire de 3^{ème} année ENITEF.
- BOUVET, J.-M. (1991): Analyse des tests clonaux d'eucalyptus hybrides, réflexions sur la méthodologie de sélection. Report of Master of sciences, INAPG, Paris.
- BOUVET, J. M. (1995): Evolution de la variabilité avec l'âge et corrélation juvénile-adulte dans les populations d'eucalyptus. Thèse de doctorat INAPG. 296 p.
- BOUVET, J.-M. and H. BAILLERES (1995): Expression of some Growth and Wood properties Traits Among *Eucalyptus urophylla* x *grandis* clones in Congo. Proceedings de la conférence CRCTHF-IUFRO: Eucalypt plantation: improving fibre yield and quality. Hobart, Australie 19–24 février 1995, pp. 89–92.
- BOUVET, J.-M. and P. VIGNERON (1996): Variance Structure in *Eucalyptus* Hybrid Populations, *Silvae Genetica* **45**: 2–3.
- BOUVET, J. M., P. VIGNERON, A. SAYA and R. GOUMA (2003): Trends in variances and heritabilities with age for growth traits in eucalyptus spacing experiments. *Silvae genetica* **52**, 3–4: 121–133.
- BOUVET, J. M., P. VIGNERON and A. SAYA (2005): Phenotypic plasticity of growth trajectories and ontogenic allometry in response to density in eucalyptus clones and families. *Annals of Botany* **96**: 811–821.
- BOUVET, J. M., P. VIGNERON and A. SAYA (2009): Trends in additive, dominance and environmental effects with age for growth traits in *Eucalyptus* hybrid populations. *Euphytica* **165**: 35–44.
- DALE, G. and M. DIETERS (2007): Economic returns from environmental problems: Breeding salt- and drought-tolerant eucalypts for salinity abatement and commercial forestry. *Ecological Engineering* **31** (2007) 175–182.
- DE ASSIS, T. F. (2000): Production and use of eucalyptus hybrids for industrial purposes. Pages 63–74. *In*: H. S. DUNGEY, M. J. DIETERS and D. G. NIKLES, editors. Hybrid Breeding and Genetics of Forest Trees Proceedings of QFRI/CRC-SPF Symposium. Department of Primary Industries, Brisbane, Noosa, Queensland, Australia.
- FALCONER, D. S. and T. F. C. MACKAY (1996): Introduction to quantitative genetics. New York; Longman Scientific and technical, 4th ed., 464 p.
- FRANKLIN, E. C. (1979): Model relating levels of genetic variances to stand development of four North American conifers. *Silvae Genetica* **28**: 207–212.
- GALLAIS, A. (1989): Théorie de la sélection en amélioration des plantes. Editions Masson, Paris. 589 p.
- JOHNSON, G. R., R. A. SNIEZKO and N. L. MANDEL (1997): Age trends in Douglas-fir genetic parameters and implication for optimal selection age. *Silvae Genetica* **46**: 349–358.
- LEE, S. J., J. C. WOOLLIAMS, J. A. SAMUEL and D. C. MALCOM (2002): A study of population variation and inheritance in Sitka spruce: III. Age trends in genetic parameters and optimum selection ages for wood density, and genetic correlations with vigour traits. *Silvae Genetica* **51**: 143–151.
- LEE, D. J., J. R. HUTH, J. T. BRAWNER and G. R. DICKINSON (2007): Relative performance of Corymbia Hybrids and parental open-pollinated families in subtropical Queensland. In conference on "Eucalypts and diversity: balancing productivity and sustainability". Durban 22 to 26/10/2007.
- LOPEZ, G. A., B. M. POTTS, G. W. DUTKOWSKI, J. M. RODRIGUEZ TRAVERSO (2001): Quantitative genetics of *Eucalyptus globulus*: affinities of land race and native stand localities. *Silvae Genetica* **50**: 244–252.
- MARQUES, O. G., H. B. ANDRADE and M. A. P. RAMALHO (1996): Assessment of the early selection efficiency in *Eucalyptus cloeziana* F. MUELL. in the northwest of Minas Gerais state (Brazil). *Silvae Genetica* **45**: 359–361.
- MEYERS, R. H. and D. G. MONTGOMERY (2002): Response surface methodology – Process and product optimization using designed experiments. Wiley series in probability and statistics. Wiley. 824 P.
- OSORIO, L. F., WHITE, T. L and D. A. HUBER (2003): Age-age and trait-trait correlations for *Eucalyptus grandis* Hill ex Maiden and their implication for optimal selection age and design of clonal trials. *Theoretical and Applied Genetics* **106**: 735–743.
- PATINOT-VALERA, F. and P. Y. KAGEYAMA (1995): Parametros geneticos y espaciamiento en progenie de *Eucalyptus saligna* Smith. Research Paper IPEF, Piracicaba (48/49): 61–76, jun. Dez 1995.
- POTTS, B. M. and H. S. DUNGEY (2004): Interspecific hybridization of *Eucalyptus*: key issues for breeders and geneticists. *New Forests* **27**: 115–138.

- REZENDE, G. D. S. P. and M. D. V. DE RESENDE (2000): Dominance effects in *Eucalyptus grandis*, *Eucalyptus urophylla* and Hybrids. In: DUNGEY, H. S., DIETERS, M. J. and NIKLES, D. G. (Eds.). Hybrid Breeding and Genetics of Forest Trees. Proc. QFRI/CRC-SPF Symposium, Noosa, Queensland, Australia. April 2000. p93–100.
- RETIEF, E. C. L. and T. K. STANGER (2007): Genetic parameters of pure and Hybrid populations of *Eucalyptus grandis* and *Eucalyptus urophylla* and implications for Hybrid breeding strategy. In: conference on “Eucalypts and diversity: balancing productivity and sustainability”. Durban 22 au 26/10/2007
- SANUHEZA, R. P., T. L. WHITE, D. A. HUBER and A. R. GRIFFIN (2002): Genetic parameters estimates, selection indices and predicted genetic gains from selection of *Eucalyptus globulus* in Chile. *Forest Genetics* **9**: 19–29.
- SAS INSTITUTE INC. (1990): SAS/STAT user's guide, release 6.03 edn. SAS Institute Inc, Gary, North Carolina.
- TIBBITS, W. and G. HODGE (1998): Genetic parameter and breeding value predictions for *Eucalyptus nitens* wood fiber production traits. *Forest Science* **44**: 587.
- VELILLA, E. L., G. W. DUTKOWSKI and R. P. SANUHEZA (2007): Genetic analysis of *Eucalyptus nitens*: Genetic parameters and breeding value predictions In conference on “Eucalypts and diversity: balancing productivity and sustainability”. Durban 22 au 26/10/2007.
- VERRYN, S. D. (2000): *Eucalyptus* hybrid breeding in South Africa. In: DUNGEY, H. S., DIETERS, M. J. and NIKLES, D. G. (Eds.). Hybrid Breeding and Genetics of Forest Trees. Proc. QFRI/CRCSPF Symposium, Noosa, Queensland, Australia. April 2000. p191–199.
- VIGNERON, P. (1991): Creation et amelioration de varietes hybrides d'Eucalyptus au Congo. In: SCHÖNAU, A. P. G. (Ed.). The Role of Eucalypts. Proc. IUFRO Symposium on Intensive Forestry: Durban, South Africa. September 1991. p345–360.
- VIGNERON, P. and J.-M. BOUVET (1997): *Eucalyptus* In Breeding of tropical plants. In: CHARRIER, A., JACQUOT, M., HAMON, S., NICOLAS, D. (Ed.) Cirad, Orstom, Montpellier, Collection Repères. pp. 267–290.
- VIGNERON, P., J. M. BOUVET, R. GOUMA, A. SAYA, J. M. GION and D. VERHAEGEN (2000): Eucalypt hybrids breeding in Congo. Pages 14–26. In: H. S. DUNGEY, M. J. DIETERS, and D. G. NIKLES, editors. Hybrid breeding and genetics of forest trees. Proceedings of QFRI/CRCSPF Symposium. Department of Primary Industries, Brisbane, Noosa, Queensland, Australia.
- VOLKER, P. W. (1995): Evaluation of *Eucalyptus nitens* x *globulus* for commercial forestry. Pages 222–225. In: B. M. POTTS, editor. Eucalypt plantations: Improving fibre yield and quality. CRCTHF-IUFRO, Hobart, Australia.
- VOLKER, P. W., C. A. DEAN, W. N. TIBBITS and I. C. RAVENWOOD (1990): Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. *Silvae Genet* **39**: 18–21.
- WEI, X., and N. M. G. BORRALHO (1998): Genetic control of growth traits of *Eucalyptus urophylla* S. T. BLAKE in South East China. *Silvae Genetica* **47**: 158–164.

Genetic Parameters and Genotype by Environment Interactions for Green and Basic Density and Stiffness of *Pinus radiata* D. Don Estimated Using Acoustics

By B. WIELINGA^{1),5)}, C. A. RAYMOND^{2),4),*}, R. JAMES¹⁾ and A. C. MATHESON^{3),4)}

(Received 5th February 2008)

¹⁾ Fenner School of Environment and Society, Australian National University, Canberra ACT 0200.

²⁾ Forests NSW, PO Box 46, Tumut NSW 2720. Current Address: Centre for Plant Conservation Genetics, Southern Cross University, PO Box 157, Lismore NSW 2480.

³⁾ Current Address: Post Retirement Research Fellow, CSIRO Plant Industry, PO Box 1600, Canberra ACT 2601.

⁴⁾ Visiting Fellow, Fenner School of Environment and Society, Australian National University, Canberra ACT 0200.

⁵⁾ Current Address: Carter Holt Harvey Wood Products Australia, PO Box 330, Mount Gambier SA 5290.

*) Corresponding Author, E-mail: Carolyn.raymond@scu.edu.au

Abstract

Genetic parameters and genotype by environment interactions for wood properties of 13-year-old *Pinus radiata* were determined by sampling two progeny trials on contrasting sites in the southern slopes of New South Wales, Australia. Heritability of green and basic density were determined together with dynamic modulus of elasticity (MOE) measured using TreeTap.

The phenotypic variance in MOE (CV 17–18%) was almost three times that of basic density. MOE and basic density were highly heritable at both sites (h^2 0.57 & 0.79 for MOE & 0.59 and 0.85 for density). There was a